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Title: Arboreal spiders in coffee agroecosystems: Untangling the web of local and landscape influences driving diversity

Authors: Zachary Hajian-Forooshani[1], David J. Gonthier[2], Linda Marin[2], Aaron L. Iverson[1], and Ivette Perfecto[2]

Affiliations: 1. Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI, United States 2. School of Natural Resources and Environment, University of Michigan, Ann Arbor, MI, United States

Corresponding author: Zachary Hajian-Forooshani. (269) 420-6640 zhajianf@umich.edu

Abstract: Agricultural intensification is implicated as a major driver of global biodiversity loss. Local management and landscape scale factors both influence biodiversity in agricultural systems, but there are relatively few studies to date looking at how local and landscape scales influence biodiversity in tropical agroecosystems.

Understanding what drives the diversity of groups of organisms such as spiders is important from a pragmatic point of view because of the important biocontrol services they offer to agriculture. Spiders in coffee are somewhat enigmatic because of their positive or lack of response to agricultural intensification. In this study, we provide the first analysis, to our knowledge, of the arboreal spiders in the shade trees of coffee plantations.

In the Soconusco region of Chiapas, Mexico we sampled across 38 sites on 9 coffee plantations. Tree and canopy connectedness were found to positively influence overall arboreal spider richness and abundance. We found that different functional groups of spiders are responding to

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different local and landscape factors, but overall elevation was most important variable influencing arboreal spider diversity.

Our study has practical management applications that suggest having shade grown coffee offers more suitable habitat for arboreal spiders due to a variety of the characteristics of the shade trees. Our results which show consistently more diverse arboreal spider communities in lower elevations are important in light of looming global climate change. As the range of suitable elevations for coffee cultivation shrinks promoting arboreal spider diversity will be important in sustaining the viability of coffee.

Keywords: agroecosystem, coffee, arboreal spiders, biodiversity, shade trees, management, climate change

Introduction

Agriculture has the potential to play a pivotal role in the conservation of biodiversity worldwide, and with 40% of the terrestrial Earth fragmented by agriculture (Foley et al. 2005), there in lies the need to more effectively manage agroecosystems for both food production and biodiversity conservation. With growing concerns about the adverse effects of modern agriculture (Foley et al. 2005; Swift et al. 2006; IAASTD 2009; Rockström et al. 2009; Power 2010), by making agroecosystems more habitable to biodiversity we can simultaneously address the global decline in biodiversity while maintaining sustainable agricultural production.

Biodiversity in agroecosystems responds to local factors such as crop density and crop diversity, crop rotations, and chemical inputs (Tscharntke et al. 2005, Batáry 2010). Biodiversity can also respond to landscape scale factors such as distance to forest, management of edge habitat, and landscape heterogeneity (Tscharntke et al. 2005, Schmidt 2005). Some species response to different scales of management intensity, (Tscharntke et al. 2005, Drapela 2007, Batary 2008) therefore management at local and landscape levels can have varying impacts depending on the species.

Coffee agroecosystems in the tropics, when traditionally managed with high numbers of shade trees, tend to harbor more biodiversity then intensive coffee agroecosystems (Perfecto et al. 1996). Intensification of coffee often consists of the reduction in the number of shade trees, tree diversity, canopy complexity, as well as the increase in agrochemical inputs. Recent studies in agroforestry systems, such as coffee and cacao, show that increased biodiversity often provides greater biological control of insect pests and diseases (DeBeenhouwer et al. 2013). In cacao plantations, for example, managing for high densities of shade trees can increase the abundance of important generalist predators, especially spiders (Stenchly et al. 2011).

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Spiders are generalist predators that can offer the important biocontrol services in agriculture (Riechert 1984, Riechert 1990, Riechert 1997, Symondson 2002). Spiders prevent and suppress pest outbreaks in arable crops (Symondson et al. 2002, Riechert 1984). They are unique among predators because they are largely generalist consumers (Wise 1993), which allows them to persist when pest numbers are low by feeding on alternative prey items within the agroecosystem (Settle 1996, Symondson 2002). In some cases diverse assemblages of spiders can provide greater pest suppression than simple assemblages (Riechert 1984, Riechert 1990, Riechert 1997, Symondson 2002). Given the importance of spiders in providing biocontrol, and therefore in reducing the need for chemical control, understanding what factors drive spider abundance and richness in agroecosystems is critical.

Surprisingly in coffee, spiders show an inconsistent response to intensification and typically tend to increase with increased intensification of the agroecosystem. For example, ground and coffee-dwelling spiders are more diverse in intensified coffee agroecosystems (Pinkus et al. 2006; Marín and Perfecto 2013). Spiders that live on tree trunks of shade trees had no relationship with canopy cover and distance to forest, but they were affected by tree trunk characteristics (Marín, personal communication). Pinkus-Rendón et al. (2006) found spider diversity in the epigean layers of coffee was negatively correlated with tree cover and plant diversity but only in the rainy season. Similarly, in cacao agroforestry systems, Stenchly et al. (2011) reported no effect of shade tree density on spiders. Spider's lack of response or positive response to shade intensification lies in contrast to how other organisms respond, and how spiders respond to intensification in arable crops in the temperate zone. Studies in arable crops show that heterogeneous landscapes and low intensity agricultural practices have a positive effect on spiders (Schmidt et al. 2008, Schmidt et al. 2005, Clough et al. 2005). Spiders in tropical agroforestry systems and temperate arable crops seem to be responding to different factors, so understanding what makes these assemblages respond differently is important. Furthermore, to our knowledge, all the studies of spiders in coffee agroecosystems to date do not include the arboreal spider assemblages, in particular the spiders inhabiting the shade tree canopies. Work by Stenchly et al. (2011, 2012) on arboreal spiders in cacao agroforests suggests that arboreal spiders may be responding differently in canopies than communities on the ground, tree trunks, and the coffee layer in coffee agroecosystems.

To better understand what factors drive arboreal spider diversity, in this study, we investigated how arboreal spiders respond to a spectrum of management and landscape characteristics at three spatial scales in coffee agroecosystems. We hypothesized that there would be important drivers of spider diversity at all three spatial scales which included tree characteristics (local scale), plot level management (broader local scale), and landscape features. At the tree level we expected that the number of canopy connections to the sample tree, as well as the leaf area would increase both abundance and richness of spiders. We hypothesized that with more canopy connectedness we observe greater spider abundance and richness because of the increase in habitat access for arboreal spiders. At the plot level we expected an increase in arboreal abundance with a greater percentage of shade in the plot and an increasing number of shade trees in the plot, which has been supported in cacao plantations in the tropics (Stenchly et al. 2011). Spiders are able to maintain populations in tropical agroecosystems year round unlike in temperate agroecosystems where they often need to colonize the agricultural plots annually from edges of agriculture fields and forest fragments due to plowing (Hogg et al. 2009). We therefore predicted there would be no effect of distance to forest at the landscape scale, which has been reported by Marín and Perfecto (in review) for leaf litter spiders in coffee and Stenchly et al. (2011) in cacao plantations. We predicted that with an increasing proportion of forest in a 1000m radius from the center of our plot there would be a decrease in spider abundance and richness, because it has been shown that unmanaged land tend to harbor more diverse communities (Batáry 2012), and we would expect spiders to remain within the forest patches and not move to the coffee patches. Elevation has been an effective predictor of spider communities in the tropics (Stenchly et al. 2011); therefore, we predicted a decrease in abundance and species richness with increasing elevation.

Methods

We conducted our study in the Soconusco region of Chiapas, Mexico across coffee plantations that ranged in elevation between 695-1273 m.a.s.l. The Soconusco landscape is dominated by coffee agriculture (94%), with small forest fragments (6%) lining some valleys and mountain ridges (Philpott et al. 2008). We located 38 sites within 9 coffee plantations that varied by management intensity within this region.

Within each site we measured tree level, site level, and landscape level factors (Table 1). Tree level factors included: tree height, branch length, branch diameter at three spots on the branch, number of leaves, number of canopies touching sampled tree and identity of those trees. The average diameter of the branch was estimated and used with branch length to calculate branch volume which was used a measure of sampling effort. The area of leaves was measured and used estimated total leaf area per branch. Local site level factors described site characteristics as they pertain to the intensity of the management of the coffee plantation; in particular percent shade cover and shade tree density. We used a Global Positioning System to map a hectare circular area around the center of a site, then documented the abundance and richness of all tree species within that area. We used Incidence-based coverage estimates (ICE) in EstimateS (Colwell 2011) to estimate the total number of tree species within a site because plot size varied between (0.8 and 1.2 ha). We measured shade cover at the center, 5m and 10m away in each cardinal direction and used the average of these measurements.

Using Geographic Information Systems (GIS) we measured landscape scale factors surrounding each site. To measure landscape composition, we digitized forests and coffee farms of varying intensity using ArcGIS 10 and utilizing a basemap of the region. Plantation boundaries were used to define rough categorizations of landscape shade management intensity based on the average percent shade cover of plantations: high- (>70%), medium- (30-70%), and low- (<30%) shade management. Some plantations had large areas of more than one category of shade intensity level. We therefore delineated these areas and categorized each area into its appropriate level. With this categorization, we calculated percent forest, low-shade, medium-shade, and high-shade coffee land-use types within 250, 500, 1000m radii surrounding each site. Our data was analyzed utilizing 1000m radii because we were interested in larger scales influence on spider diversity. We also calculated the Shannon diversity index (Σ -ln(p)p) of the habitat types.

At each site three shade trees were selected belonging to the species *Inga micheliana* or *I. rodrigueziana*, the two most common shade species in the region. Once trees were selected, two branches from each tree were cut with an extendable pole-cutter or the tree was scaled and branches lowered down. The branches were then shaken aggressively over a 1 by 1m black blanket, where spiders could be more efficiently collected. After shaking no longer produced more spiders, the branch was put down on the blanket and all of the leaves were checked for spiders, then, the number of leafs on each branch was counted. All of the spiders were stored in vials of 97% alcohol in the field.

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The specimens were sorted into morphospecies and identified to species when possible. For all reproductively mature spiders body length were measured under a dissection scope. Identification of multiple groups was assisted by Guillermo Ibarra Nuñez at El Colegio de la Frontera Sur in Tapachula, Chiapas. Spiders were broken into 5 guilds defined by Young & Edwards (1990), which included sheet-web, orb-web, matrix-web, active-wandering, and ambush-wandering. We condensed these guilds into two groups: web-building spiders and wandering spiders.

To determine which factors within the agroecosystem were strong predictors of arboreal spider abundance and richness we deployed conditional inference trees. Conditional inference trees are considered well suited to deal with complex non-linear and high-order interactions in ecological data (De'ath and Fabricus 2000). Conditional inference trees are non-parametric and are suitable for multivariate variables and arbitrary measurement scales. A binary recursive data-partitioning algorithm is used to estimate regression relationships, and conditional inference trees do not assume linearities in the response variables. Parameter instability tests are used for split selection in the tree building process (Hothorn et al. 2010). Trees were run with the 'party' package in R, which gives p-values at each node of the tree. Six total trees were run: overall arboreal spider abundance, overall arboreal spider richness, web-building spider abundance, web-building spider richness, wandering spider abundance, and wandering spider richness. Independent factors included in trees are reported in table 1. All data were analyzed in R version 2.15.0.

To further evaluate differences between species we used the results of the CIT of species richness to guide further analysis by comparing sample-based rarefaction curves (MaoTao estimations in EstimateS) of spider richness in partitions of high and low elevation. To compare differences in community composition among high and low elevations, we used this same partitioning to compare three measures of community composition. First, we used non-metric multidimensional scaling (NMDS) of the Bray-Curtis similarity index to visualize differences between site and group using 95% confidence ellipses to compare overlap. For further comparison between groups, we used analysis of similarity (ANOSIM) and non-parametric multivariate analysis of variance (NPMANOVA). Both analyzes are permutation tests that compare the pairwise differences (Bray-Curtis similarity) of sites among groups and within groups. NPMANOVA highlights if the dispersion of sites differs between groups and within groups, while ANOSIM describes whether sites within group are more similar in composition relative to sites between groups (Hämmer, 2001; Anderson, 2001).

Results

The estimated species accumulation curve approached asymptotic species richness for this arboreal spider community, suggesting our sampling had captured a significant portion of the arboreal spider community (Fig. 1).

There were 934 spiders collected in total from the sites, consisting of 109 morphospecies. Only sexually mature spiders were included in the abundance data and about 15% of the samples consisted of spiders that were not sexually mature. The composition of the canopy spider communities was comprised mainly of spiders in the families Theridiidae with 44.4% and Anyphaenidae with 20.9%. The most abundant species was *Theridion nudum* (Levi 1967) in the family Theridiidae with 168 individuals followed by *Wulfila inornatus* (O. P. Cambridge 1898) with 139 individuals and *Teudis geminus* (Petrunkevitch 1911) both in Anyphaenidae.

Overall arboreal spider abundance

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Elevation was the most important factor in driving total arboreal spider abundance ($p<0.001$; Fig. 2). At elevations at or below 920 any branches above 204 cm^3 had a higher abundance of spiders ($p<0.001$). When a branch was at or below 204 cm^3 and there were over 165 trees in the plot there was a significantly higher abundance of arboreal spiders ($p=0.037$). When there were 165 or fewer trees in a plot then the percentage of forest on a 1000m radius from the center of the plot was important. When over 1.8% of the plot was forest then there was higher arboreal spider abundance in the sampled trees ($p=0.015$).

Wandering spider abundance

As with total spider abundance elevation, elevation was the most important factor driving wandering spider abundance. At or below 920m there was a greater abundance of spiders ($p<0.001$; Fig. 3). Branches with a volume above 204cm^3 had significantly more spiders ($p=0.002$), while within sites with branches smaller than 204.2, the number of trees in the plot was the next most important driver of spider abundance. There is greater abundance of arboreal spiders when there was over 155.4 trees in a plot ($p=0.037$).

Web-building spider abundance

As with total spider abundance and wandering spider abundance, elevation was the most significant factor for web-building spider abundance. Spiders found at or below 623m had significantly higher abundance then elevations above that threshold ($p<0.001$; Fig. 4). Another threshold in elevation was found where there was greater abundance at or below 920m ($p=0.006$). Within sites below 920m, branch volume was the next most important predictor. Within sites above 920m, the number *Inga* spp. trees connecting the canopy of the sampled tree was the next most important factor.

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Overall arboreal spider richness

Elevation was also the most important factor driving arboreal spider richness ($p<0.001$; Fig. 5). At higher elevations there was lower arboreal spider richness. Above 774m shade was significant in determining spider richness ($p=0.028$). On farms with over 25% there was higher species richness. At or below 774m the size of the branch was important and branches larger than 165cm³ had higher species richness ($p=0.021$). Although the CIT reported significant differences in species richness and high and low elevation, we found no differences between the accumulation of species in sites at high or low elevations (Fig. 6).

The composition analyses of sites at high and low elevations revealed some differences in spider communities (Fig. 7). Visually there were no differences in the similarity of spider communities at high and low elevations as the 95% confidence ellipses of the NMDS overlapped substantially (Fig. 7). Further, the ANOSIM showed no difference in spider composition at high and low elevations (ANOSIM; $R = 0.0435$; $P = 0.238$). However, sites at high elevations had greater dispersion than sites at low elevations (NPMANOVA; $F = 4.86$; $P = 0.0001$).

Wandering spider richness

For wandering spider richness, elevation was not a factor; instead, the number of *Inga* spp. canopy connections was the most important factor in determining the richness of wandering spiders. Where there were more than two *Inga* spp. canopy connections greater richness was observed ($p=0.005$; Fig. 8). For trees with two or less *Inga* spp. connections habitat heterogeneity at the landscape level (Shannon index) was important. Landscapes with index values of 1.05 or less had higher wandering spider richness ($p=0.026$).

Web-building spider richness

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Species richness of web-building spiders was highest at sites with elevation at or below 811m. At elevations higher then 811m, branch size was important, and branches above 176cm³ had higher web-building spider species richness (p=0.007; Fig. 9). On those branches larger than 176cm³ having more than one *Inga* spp. canopy connection leader to greater web-building spider richness (p=0.031). The percentage of forest in a site had an effect on web-building spider richness when sampled branches were at or below 176m³ (p=0.038). When 0.106% or less was forest there was greater web-building spider richness.

Discussion

This is the first study to sample canopy spiders in coffee plantations. We found that different groups of spiders are affected in different ways by tree, plot and landscape level factors. Branch size was consistently important in predicting arboreal spider abundance and can be taken as measures of sampling effort across the sampled sites, but this can be informative since both measures can be useful when determining management practices across the coffee plantations. There is extensive trimming of shade trees across almost all of the plantations and these results suggest more robust tree canopies lead to greater overall arboreal spider abundance and richness.

With the exception of the wandering spider species richness, elevation was the strongest and most consistent predictor of arboreal spider abundance and species richness. With increasing elevation we found a decrease in both abundance and species richness. The elevation gradient in species richness has been well studied for many organisms (reviewed by Willing et al. 2003 and Hudkinson 2005) including spiders (Otto and Svensson 1982; Urones and puetro 1988; Olson 1994; Russell-Smith and Stork 1994; Rahbek 1995; Bowden and buddle 2010; Stenchley et al. 2011). Although a number of studies have found a negative relationship between ground dwelling spider species richness and abundance and elevation (Otto and Svensson 1982; Rushton and Eyre 1992; Chatzaki et al. 2005), others have found no effects or an increase in the abundance of certain groups (Urones and Puerto 1988; Russell-Smith and Stork 1994; Chatzaki et a al. 2005. For example Stenchly (2011), studied web building spiders in cacao plantations in Indonesia and reported a positive relationship between spider abundance and elevation. The inconsistencies in distribution pattern could be due to the variability of elevational ranges and types of spiders included in the studies, as well as the potential impact of other variables such as habitat types and landscape heterogeneity. In our study, the lack of response for wandering spider richness suggests that this group of spiders is less sensitive to elevational gradients.

We found some support for our expectation of increased spider abundance and richness with greater shade cover and tree density management. At the plot level, 25% shade cover significantly increased overall arboreal spider richness. The number of trees per plot had a positive effect on the overall arboreal spider abundance, and abundance of wandering spiders. *Inga* spp. trees tend to be the most common trees in many of the coffee plantations in the region because of their association with nitrogen fixing bacteria (Moguel and Toledo 1999). In some of the more intensive plantations they account for around 40% of the non-crop trees. Web-building arboreal spider abundance and the richness increased with the number of *Inga* spp. tree connections to the focal tree.

Overall, landscape level effects were absent or weak in our study. Similar to what Stenchly and colleagues found for web spiders in cacao plantations in Indonesia, we did not detect any effect of distance to forest, and this is likely because the coffee agroecosystem offers habitat architecturally similar to the forest. Although never the most explanatory variable, the proportion of forest surrounding sites did have some minor impacts on spiders. The proportion of forest in the landscape positively correlated with the abundance of all arboreal spiders and a negatively correlated with the richness of web-builders. In the case of the overall abundance of arboreal spiders the positive effect was found only at lower elevation site (below 920 m), lower branch volume (≤ 204 cm3) and in plots with lower tree density (≤ 165.5 individuals). It seems that, at lower elevations, where spiders are more abundance, and under conditions of lower vegetation density (more intensive sites), the forest acts as a source for arboreal spiders. The lower richness in web-building spiders with larger proportion of forest was observed only at higher elevations (>811m) where spider abundance and richness was low, and for lower branch volumes suggesting that at higher elevations web-building spiders are more forest specialists and don't more much into coffee plantation. Land use heterogeneity has been shown to be important to arboreal spider communities in tropical agroforestry systems (Stenchly et al. 2011), and we detected a negative effect on wandering spider richness with an increase in land use heterogeneity.

The surprisingly large and consistent effect of elevation across most groups of arboreal spiders can have very important implications in light of climate change. Arboreal spiders were consistently higher in abundance and richness in lower elevations, and as the range of elevation for coffee cultivation dwindles the services provided by spiders may become more important. It is estimated that within a 2 degree Celsius change in global temperature there would be a 400m elevational shift in suitable coffee growing elevational range (Vermeulen et al. 2013). Our results suggest that as less coffee is grown in lower elevations, the pest control services of the greater diversity and abundance of spiders will be lost to coffee production. Not only will climate change shift suitable elevation for coffee growth but also it can add stress on coffee growers from a number of different reasons. One of the most globally important pests of coffee, the coffee berry borer, thrives in the higher temperatures assured by global climate change (Jaramillo et al. 2011). In the foreseeable future there will be new limitations on the elevation ranges of coffee cultivation along with possibilities of increased pest densities. The increased berry abundance and decreased spider pest control services will likely result in strong negative pressures on coffee.

In the light of future hardship, proactive management practices can be set into motion that will promote abundance and diversity of arboreal spiders and make coffee more resilient to global climate change. Having more trees, greater canopy cover and greater canopy connectivity results in more abundance and richness in arboreal spider communities. Not only do these management practices increase arboreal spider diversity, but also an emphasis on high shade grown coffee can lead to more than a 10% coffee berry production increase and a consistently cooler microclimate within the coffee agroecosystem (Jaramillo et al. 2013). This cooler and less variable microclimate in shade coffee leads to lower proportions of coffee berries infested by the coffee borer then on sun grown coffee plantations (Jaramillo et al. 2013).

This study demonstrates that coffee agroecosystems with more trees, greater canopy cover, and greater canopy connectivity harbor greater abundance and richness in spider communities, particularly at lower elevation where spider richness and abundance tends to be higher. This has practical management applications that suggest having shade grown coffee offers more suitable habitat for arboreal spiders due to a variety of the characteristics of the shade trees. Our results showing consistently more diverse arboreal spider communities in lower elevations is important in light of looming global climate change. As the range of suitable elevations for coffee cultivation shrinks promoting arboreal spider diversity will be important in sustaining the viability of coffee.

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Figure 1

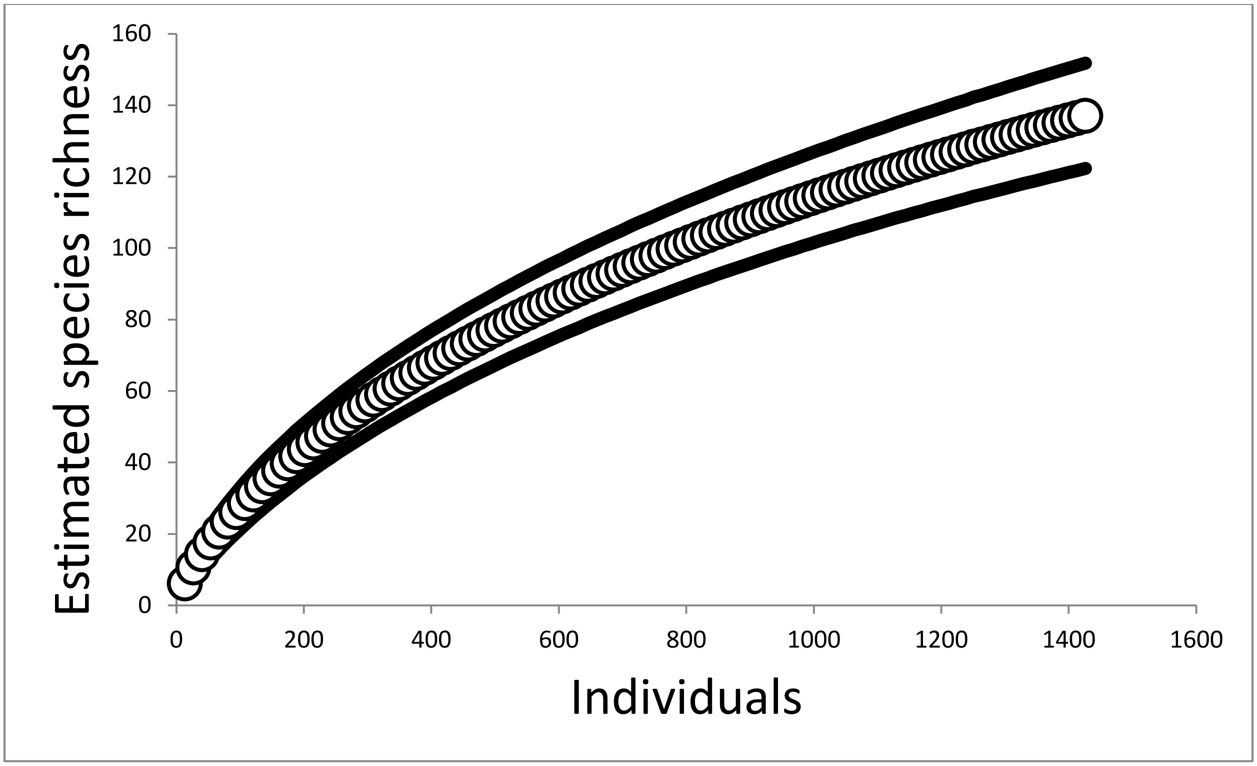

Figure 1. Estimated species accumulation across all samples. The solid lines represent 95% confidence intervals.

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Figure 2

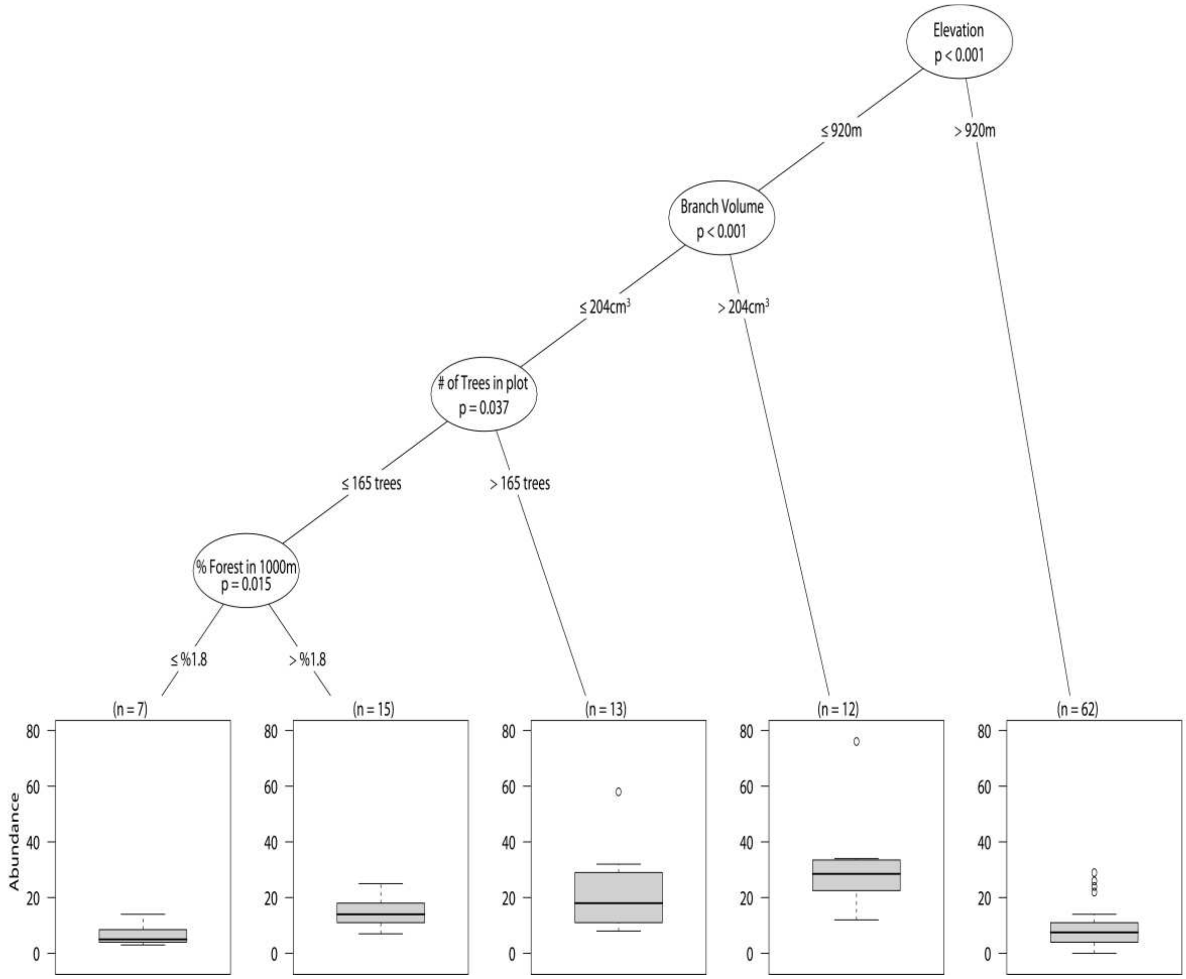

Figure 2. Conditional inference tree of total spider abundance. The p-values are listed on each node inside of the encircled explanatory variable which responded strongest to total spider abundance. The inner-quartile range of the data is shown in the box plot where the dark horizontal line shows the median and the whiskers show 1.5x inner-quartile range. Circles above the whisker show points that fall beyond 1.5x inner-quartile range. The number of data points (n) is shown above each box plot.

Figure 3

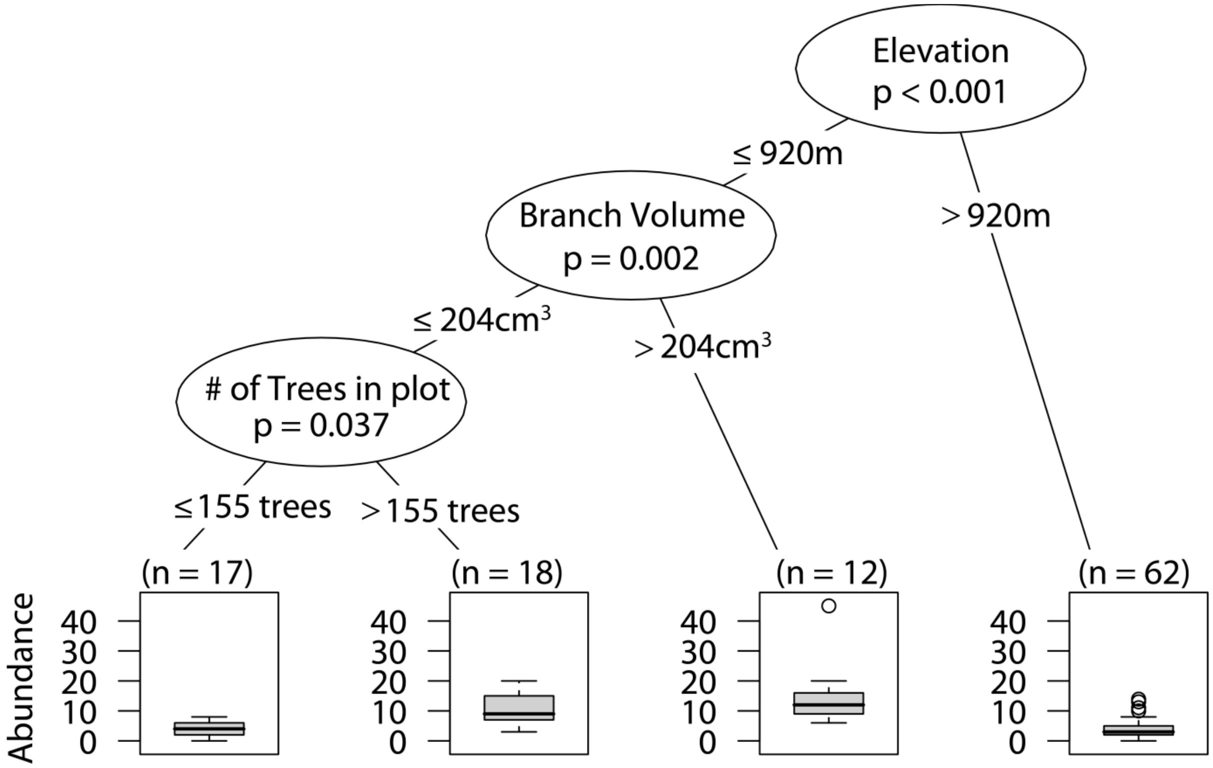

Figure 3. Conditional inference tree of web-building spider abundance. The p-values are listed on each node inside of the encircled explanatory variable which responded strongest to web-building spider abundance. The inner-quartile range of the data is shown in the box plot where the dark horizontal line shows the median and the whiskers show 1.5x inner-quartile range. Circles above the whisker show points that fall beyond 1.5x inner-quartile range. The number of data points (n) is shown above each box plot.

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Figure 4

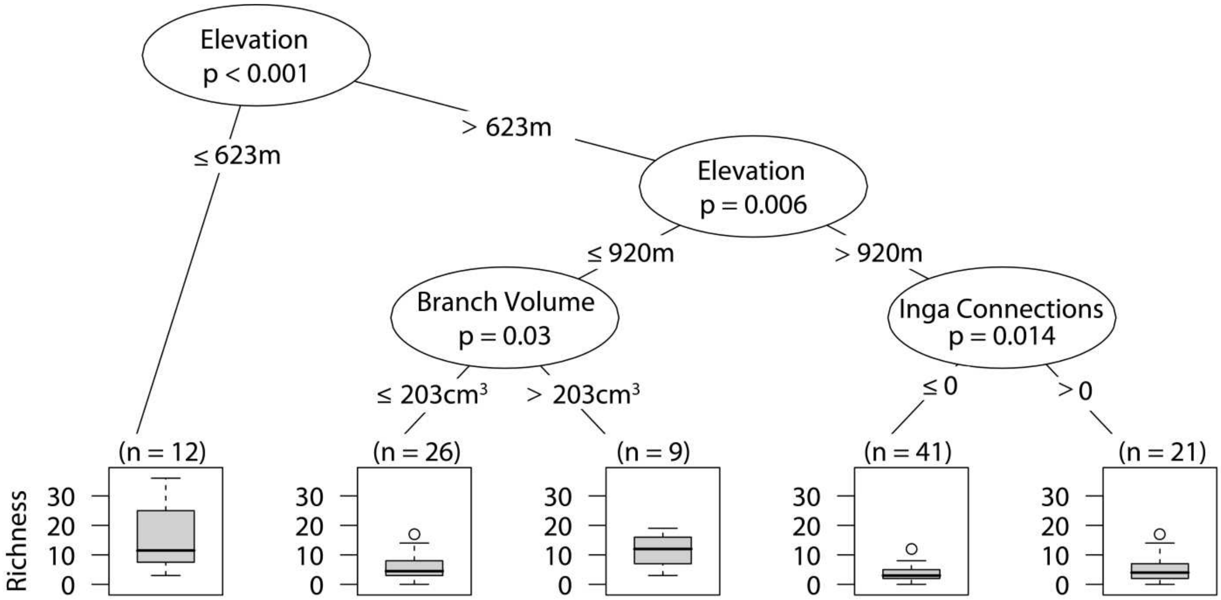

Figure 4. Conditional inference tree of wandering spider abundance. The p-values are listed on each node inside of the encircled explanatory variable which responded strongest to wandering spider abundance. The inner-quartile range of the data is shown in the box plot where the dark horizontal line shows the median and the whiskers show 1.5x inner-quartile range. Circles above the whisker show points that fall beyond 1.5x inner-quartile range. The number of data points (n) is shown above each box plot.

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Figure 5

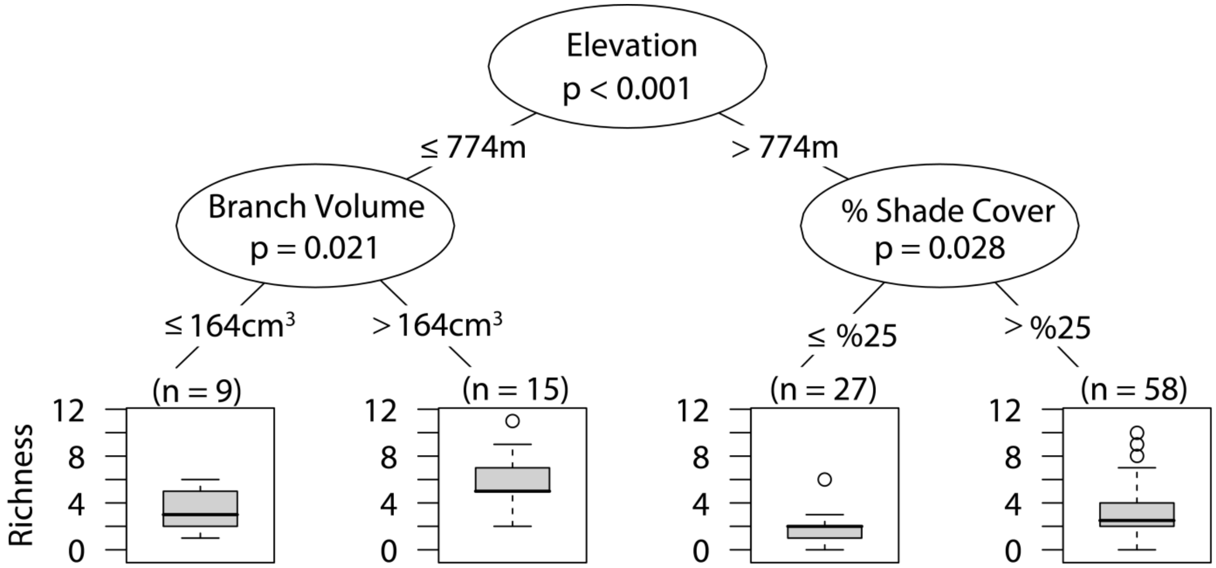

Figure 5. Conditional inference tree of total spider richness. The p-values are listed on each node inside of the encircled explanatory variable which responded strongest to total spider richness. The inner-quartile range of the data is shown in the box plot where the dark horizontal line shows the median and the whiskers show 1.5x inner-quartile range. Circles above the whisker show points that fall beyond 1.5x inner-quartile range. The number of data points (n) is shown above each box plot.

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Figure 6

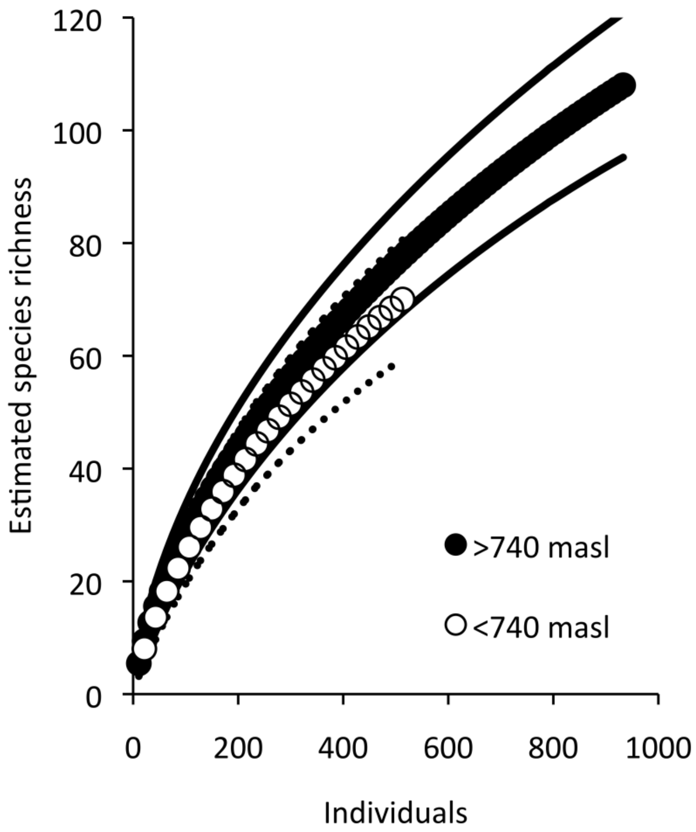

Figure 6. Estimated species accumulation curves for high elevation sites (black; >740 masl) and low elevation sites (white; <750 masl). The thin solid lines and dotted lines represent 95% confidence intervals for high and low elevation sites respectivly.

Figure 7

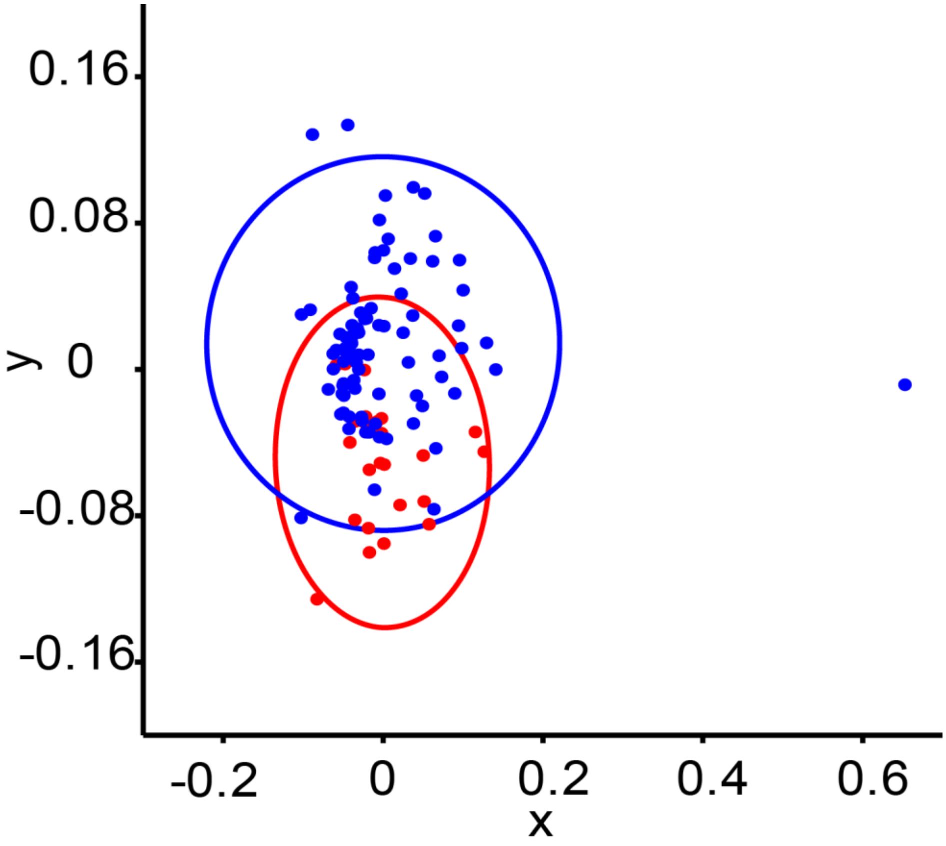

Figure 7. Non-metric multidimensional scaling for high elevation sites (blue; >740 masl) and low elevation sites (red; <750 masl). The x and y are unit-less axes. The blue and red ellipses correspond to high and low elevation 95% confidence ellipses respectively.

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Figure 8

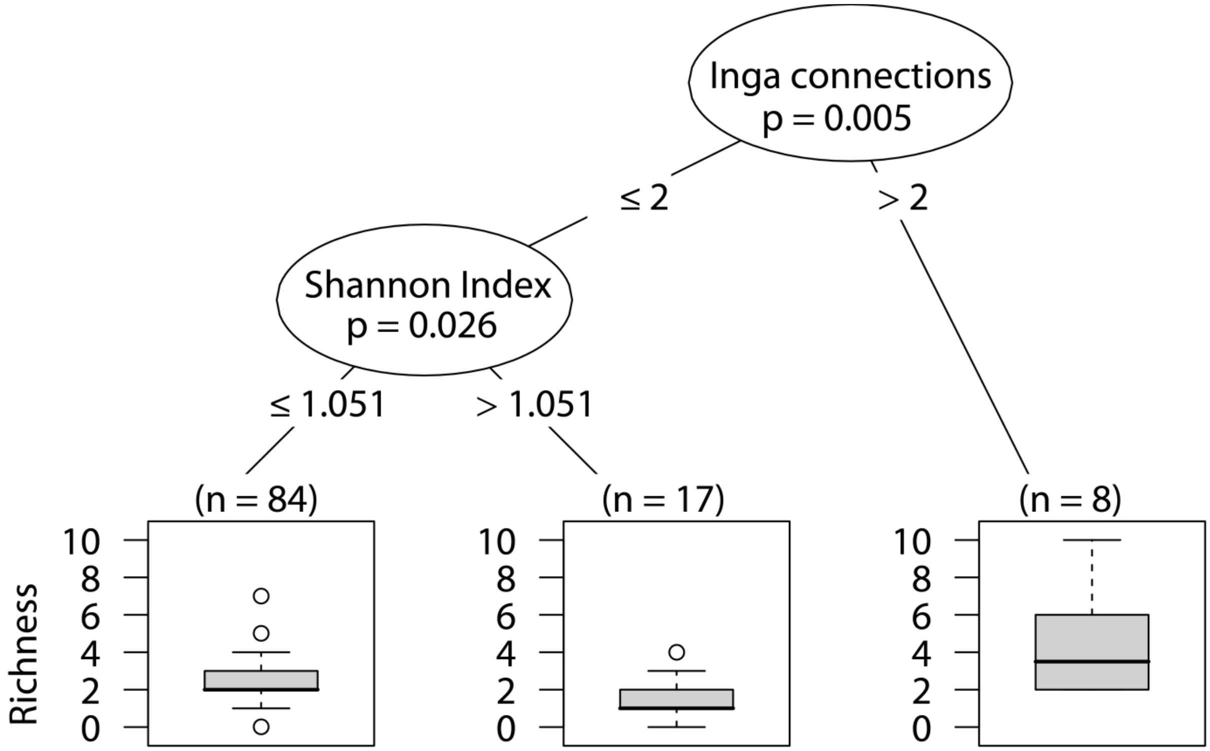

Figure 8. Conditional inference tree of web-building spider richness. The p-values are listed on each node inside of the encircled explanatory variable which responded strongest to web-building spider richness. The inner-quartile range of the data is shown in the box plot where the dark horizontal line shows the median and the whiskers show 1.5x inner-quartile range. Circles above the whisker show points that fall beyond 1.5x inner-quartile range. The number of data points (n) is shown above each box plot.

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Figure 9

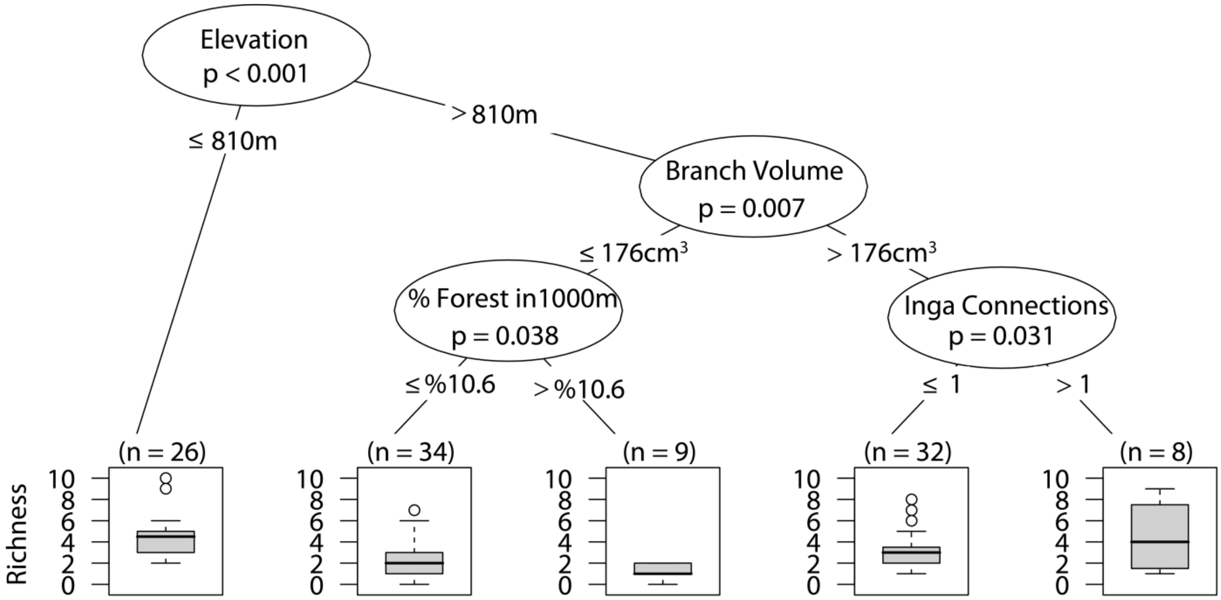

Figure 9. Conditional inference tree of wandering spider richness. The p-values are listed on each node inside of the encircled explanatory variable which responded strongest to wandering spider richness. The inner-quartile range of the data is shown in the box plot where the dark horizontal line shows the median and the whiskers show 1.5x inner-quartile range. Circles above the whisker show points that fall beyond 1.5x inner-quartile range. The number of data points (n) is shown above each box plot.

Table 1. Mean, minimum, and maximum values for tree level factors, plot level management factors, and landscape level factors.

	min	max	mean
Tree Scale			
height	400cm	1700cm	743cm
CBH	20cm	206cm	74cm
# of connections	0	6	1.3
branch volume	40cm^3	460cm^3	190cm^3
leaf area	9692cm^2	73549cm^2	31164cm^2
Plot Scale			
shade cover	2.5%	94%	94%
plot area	0.8h	1.1h	1.0h
total trees	57	312	169
trees per area	63	337	169
Landscape Scale			
% forest in 1000m	0	18%	7%
% low intensity agriculture in 1000m	0	90%	30%
%med intensity agriculture in 1000m	0	90%	40%
%high intensity agriculture in 1000m	0	90%	30%
Distance to forest	60m	870m	321m
Landscape heterogeneity in 1000m	0.17	15	1
Elevation	595m	1273m	942m